The Latitudinal Diversity Gradient: Novel Understanding through Mechanistic Eco-evolutionary Models

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Abstract: The latitudinal diversity gradient (LDG) is one of the most widely studied patterns in ecology, yet no consensus has been reached about its underlying causes. We argue that the reasons are the verbal nature of existing hypotheses, the failure to mechanistically link interacting ecological and evolutionary processes to the LDG, and the fact that empirical patterns are often consistent with multiple explanations. To address this issue, we synthesize current LDG hypotheses, uncovering their eco-evolutionary mechanisms, hidden assumptions, and commonalities. Furthermore, we propose mechanistic eco-evolutionary modeling and an inferential approach that makes use of geographic, phylogenetic, and trait-based patterns to assess the relative importance of different processes for generating the LDG.

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The latitudinal diversity gradient - novel understanding through mechanistic eco-evolutionary models

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Abstract

The latitudinal diversity gradient (LDG) is one of the most widely studied patterns in ecology, yet no consensus has been reached about its underlying causes. We argue that the reasons are the verbal nature of existing hypotheses, the failure to mechanistically link interacting ecological and evolutionary processes to the LDG, and the fact that empirical patterns are often consistent with multiple explanations. To address this issue, we synthesize current LDG hypotheses, uncovering their eco-evolutionary mechanisms, hidden assumptions, and commonalities. Furthermore, we propose mechanistic eco-evolutionary modeling and an inferential approach that makes use of geographic, phylogenetic, and trait-based patterns to assess the relative importance of different processes for generating the LDG.

State of the art and calls for novel mechanistic approaches

The increase in species diversity from the poles to the equator, commonly referred to as the latitudinal diversity gradient (LDG), is one of the most pervasive [1, 2] and widely debated biological patterns, with at least 26 listed hypotheses associated with it [3-5]. These hypotheses can be classified into three higher-level categories related to latitudinal variation in **ecological limits** (See Glossary), **diversification rates**, and time for species accumulation (Table 1). Empirical evidence seems compatible with many of these hypotheses. For example, species richness is correlated with purported proxies for ecological limits such as net primary productivity [6-8], diversification rate can vary latitudinally due to gradients in temperature [9, 10], and diversity is greatest in regions where diversification has occurred over a longer period [11-13]. These and similar studies have improved our understanding of the LDG and macroevolutionary patterns in general, but the diffuse support for different hypotheses reveals a lack of consensus and points to challenges in testing and evaluating these hypotheses.

77 We argue that reconciling the causes of the LDG requires moving beyond verbal chains of
78 logic, which are inherently prone to error with respect to how assumptions result in their
79 predicted effect [14], and towards a more formal and mechanistic framework. Verbal
80 hypotheses often contain hidden assumptions that go untested and lack specificity with
81 respect to the mechanistic underpinning of relevant **ecological** and **evolutionary processes**.
82 Verbal hypotheses also tend to focus on a single driver to predict just one or a few patterns
83 related to that driver. Consequently, these predictions alone may not be sufficient to
84 distinguish competing hypotheses [15, 16]. A more explicit description of the processes
85 underlying all hypotheses will generate a wider range of predictions which can be used to
86 disentangle possibly non-mutually exclusive hypotheses and evaluate the relative importance
87 of these processes.
88
89 We, therefore, call for a transformation in the way biologists think about and study the LDG.
90 The classification of hypotheses (Table 1) is an important first step, but it does not resolve the
91 difficulty of identifying and quantifying the relative strength of the processes underlying the
92 LDG. We propose moving towards a mechanistic framework, founded on key processes that
93 describe how individual organisms interact with their biotic and abiotic environments, and
94 how these interactions scale up to result in the LDG and other **secondary biodiversity**
95 **patterns**. Ultimately, revealing the nature of these **eco-evolutionary processes** will yield
96 more insight than continuing to argue about non-mutually exclusive LDG hypotheses.
97
98 ## Examining the LDG through the lens of mechanistic macroecology
99 ### Key processes across levels of biological organization
100 We recognize four key processes, as defined by [17], that necessarily underpin the LDG and
101 thus should be included as components of any LDG model that aims to capture variation in
102 species richness, abundance, and composition over a spatially and temporally variable

environment: 1) selection, 2) ecological drift, 3) dispersal, and 4) speciation. Selection, drift, and dispersal can all influence the birth, death, and movement of individuals over small spatial and temporal scales. Selection (sensus [17]) encompasses any process that results in the differential survival and reproduction of individuals, based on how **environmental filtering** [18] and biotic interactions select for specific traits. Ecological drift manifests itself via stochastic variation in the births and deaths of individuals. Dispersal of individuals is influenced by the spatial structure of the landscape as well as individual dispersal capabilities and can lead to species colonizing new regions. Each of these individual-level ecological and microevolutionary processes is propagated throughout higher levels of biological organization, resulting in discrete patterns at the level of populations, species, and communities (Figure 1).

Over longer timescales, environmental conditions have fluctuated with glacial/interglacial oscillations, cooler and warmer periods in Earth's history, orogenic events, volcanic activity, and shifts in tectonic plates, all of which can affect diversity dynamics [19-21]. At these spatial and temporal scales selection, ecological drift, and dispersal determine where species or even whole clades are able to persist geographically and how traits evolve. Species that become poorly adapted to the environment or that are poor competitors for resources are expected to have low fitness and ultimately go extinct, reflecting critical eco-evolutionary feedbacks [22, 23]. Speciation becomes especially relevant with increasing temporal and spatial scales. The details of how speciation occurs are complex and the critical question in a LDG context becomes how and why speciation mode or rate varies along geographic gradients. All of the processes described above necessarily interact with each other and with the spatiotemporal environment, resulting in the broad range of geographic and phylogenetic biodiversity patterns that we observe today. As highlighted below, these processes can help us compare and disentangle LDG hypotheses.

Classical LDG hypotheses revisited

Characterizing LDG hypotheses based on the key processes described above helps to clarify the internal logic of those hypotheses, and highlights how they differ. All hypotheses invoke an explicit driver or condition that varies latitudinally (Figure 1), but considering the processes related to this driver, often below the level of biological organization at which the hypothesis was formulated, can reveal previously unrecognized assumptions and predictions. Below we discuss four examples, chosen to represent hypotheses invoking variation in limits, rates, and time. These examples may also serve as a guide for better understanding other hypotheses.

The more individuals hypothesis

The "more individuals hypothesis" invokes latitudinal variation in ecological limits and a positive relationship between the number of species and resource availability [24]. If resources are finite and a zero-sum constraint on the total amount of biomass or individuals applies, any increase in diversity over time results in a decrease in average biomass or abundance per species. Extinction rates will thus be diversity-dependent and richness will be regulated around some equilibrial value that scales with the total number of individuals that can be supported [24, 25]. This hypothesis implicitly invokes interspecific competition and the resultant allocation of resources across species (Table 1). The argument does not invoke selection (Fig. 1) and can be applied equally to ecologically neutral or non-neutral species. An important and unstated assumption is that the response of the biota to environmental change is fast enough that richness is at equilibrium across the latitudinal gradient.

The seasonality hypothesis

154 The seasonality hypothesis argues that the within-year environmental stability of the tropics
155 results in either greater diversification rates or higher ecological limits via increased niche
156 packing (Table 1 and Fig. 1). The first argument suggests that in the less seasonal tropics,
157 organisms experience a smaller range of conditions and hence evolve narrower thermal niches
158 compared to the temperate zone. The idea that "mountain passes are higher in the tropics"
159 [26] suggests that dispersal barriers were effectively greater there, increasing the chance of
160 population divergence and allopatric speciation [27, 28]. Selection thus dictates the
161 environmental conditions that a species can tolerate, but it is speciation rate that varies with
162 latitude and ultimately generates the LDG. The second version of the seasonality hypothesis
163 suggests that stability-driven specialization promotes intense niche packing, and hence more
164 species can coexist in the tropics [29, 30]. Species are then hypothesized to evolve narrower
165 resource breadths rather than narrow thermal niches, assuming that resources are limited and
166 that diversity actually emerges from niche packing [29] (Table 1, Figure 1). Implicit in both
167 hypotheses is a performance tradeoff between specialists and generalists, such that specialists
168 evolve and outcompete generalists in aseasonal environments.
169
170 *The temperature-dependent speciation rates hypothesis*
171 The hypothesis that higher temperature elevates evolutionary rates has been used to explain
172 global diversity patterns in both land and sea [31, 32]. One version of the hypothesis [33]
173 follows from the metabolic theory of ecology [34], stating that temperature positively affects
174 all biological rates including mutation rates, which can lead to speciation and ultimately
175 diversity accumulation. This assumes that speciation rates directly follow from mutation rates,
176 which may be problematic if other factors (e.g. existence of geographic barriers, assortative
177 mating) are limiting speciation. The hypothesis makes no specific predictions regarding
178 selection or dispersal. Importantly, this hypothesis could be invoked in either an equilibrium
179 or non-equilibrium world. In a non-equilibrium world, speciation rates alone could explain

variation in richness between regions if all regions were similarly old, and extinction rates were equal across regions [10]. In an equilibrium world, increased speciation rates in the tropics can lead to higher equilibrium richness, as in Hubbell [35] neutral model of biodiversity.

The tropical niche conservatism hypothesis

The tropical **niche conservatism** hypothesis [36, 37] states that diversity is higher in the tropics because of the infrequency of colonisations of the cooler temperate zone by a tropical ancestor due to strongly conserved thermal niches and tropical origins of most taxa, and hence the longer time available for diversification in the tropics. The hypothesis assumes that, barring major disturbances or climatic shifts, species richness will continue to increase unbounded over time [37]. This hypothesis has only ever been formulated at the species level, and yet it inherently implies a particular set of rules by which individuals interact with the environment and each other. Selection by the environment is by definition strong, with individuals unable to survive and reproduce under conditions different from their optima, and evolution of a new optimum is rare. Less obvious are the implications of the hypothesis for resource competition between individuals. Unbounded, or diversity-independent, diversification is only possible in the absence of an overarching zero-sum constraint [25]. The absence of such a constraint implies that while the population size of a species might be affected by the fit between the environment and environmental performance traits, it is independent of the population sizes of potential competitors and of interspecific competition more broadly.

The utility of a mechanistic framework

The examples presented above illustrate three insights gained by adopting a generalized eco-evolutionary framework. First, many of the fundamental rules by which organisms are

assumed to interact with each other and with their environment will be qualitatively similar regardless of LDG hypothesis. For example, individual survival and reproduction must be functions of how well adapted the individuals are to their environment relative to their intra- and interspecific competitors. Second, latitudinal differences in ecological limits, diversification rates, and time for diversification may emerge via different **mechanisms** integrated into the same framework. For example, diversification rates may be higher due to the temperature-dependence of mutation rates [9, 38] or due to the increased reproductive isolation in aseasonal environments [27, 39]. Third, although each hypothesis invokes a primary driver or process, we have shown that these hypotheses also make unstated assumptions about other processes and mechanisms which need to be considered in concert to fully understand the emergence of the LDG and other macroecological and macroevolutionary patterns.

Mechanistic eco-evolutionary models as a quantitative tool for understanding LDG patterns

The mechanistic framing of processes that underpin the LDG naturally facilitates the translation from heuristic thinking to mechanistic eco-evolutionary models (Box 1). We believe that building these models will be essential to making progress on the LDG and biodiversity patterns in general because they allow quantitative analyses and predictions of the various secondary patterns. Secondary patterns are key for more powerful inference about the origin of species richness patterns. Below we provide concrete examples of components of a mechanistic LDG model and associated patterns followed by a discussion about how to use such a model for inference with the available data.

Mechanistic models for studying the LDG

The spatiotemporal environmental template

The basic driver of an LDG model is the spatiotemporal environmental template. It can be viewed as the theater in which the eco-evolutionary play unfolds, and the spatiotemporal variation in that template (Earth's climatic, geologic, and tectonic history) may be as critical to emergent diversity patterns as the mechanisms and processes governing how organisms interact and evolve [40-42]. Explaining the LDG with eco-evolutionary **simulation models**, therefore, benefits from suitable paleoenvironmental reconstructions [43] and the integration of global data sets on continental topography and paleoshorelines [44, 45].

Trait-based local population dynamics

Traits are essential for individual survival and reproduction (fitness) and mechanistic models that include interactions of organismal traits and the abiotic and biotic environment, below the level of species (i.e. at the individual, population or metapopulational level), is thus appropriate. Local population dynamics can, for example be assumed to be trait-dependent [46, 47]. One set of traits might determine an organism's fitness dictated by the abiotic environment, a different set of traits may influence relative fitness associated with the suite of potential competitors present at any point in time [48]. Such a modeling approach requires making basic assumptions that facilitate the link between environmental conditions, available resources, and ecological interactions, and population dynamics then emerge from those assumptions.

Spatial and eco-evolutionary metacommunity dynamics

For modeling eco-evolutionary metacommunity dynamics, trait-based models need to be implemented in a larger spatial context, allowing individuals to disperse over geographically relevant extents. Metacommunity dynamics will arise from eco-evolutionary feedbacks between dispersing individuals and recipient communities within the context of the

257 spatiotemporal template [49]. Evolutionary dynamics result from natural selection by both
258 abiotic and biotic conditions, ecological drift, dispersal, and speciation. Speciation can be
259 modeled using a phenomenological approach or more complex allele-based models in which
260 phenotypic trait variability is completely or partially heritable and the accumulation of genetic
261 incompatibilities may drive differentiation of daughter species (Box 2). Each of these
262 modeling components is necessary for capturing the suite of processes invoked by LDG
263 hypotheses (Box 1), they can be modeled with varying degrees of complexity and they come
264 with a set of low-level assumptions that need to be clearly stated (Box 2).
265
266 **Understanding patterns and inferring processes**
267 Above we have shown that a mechanistic mindset is useful to better understand the internal
268 logic and consequences of the different hypotheses, as well as the interactions among them. In
269 addition, a **mechanistic model** can clarify the biodiversity patterns expected under different
270 combinations of spatiotemporal environmental templates, biotic interactions, and other eco-
271 evolutionary rules [e.g. 16, 48, 50]. This ability to simulate very different worldviews of how
272 the LDG arises (e.g., "ecological limits", "niche conservatism", etc.) within the same
273 comparative framework is a critical element of our approach as different types of processes
274 modeled with varying degrees of mechanistic detail can be explored and contrasted.
275
276 Ultimately, we need mechanistic models to understand the details of the emerging eco-
277 evolutionary patterns at a sufficient resolution to be able to quantitatively confront them with
278 data. The more secondary patterns (e.g. phylogenies, species ranges, distributions of
279 abundance or functional traits) that can be modeled, the greater the diagnostic power of the
280 model for exploring parameter space and for inferring the strength and interactions of
281 different processes. The examination of these patterns will also point to the type of data that
282 will be most valuable for reliable inference of a given process [51].

While we believe that confronting different model scenarios with multiple observed patterns (described in Box 3) is the only way to make progress in understanding the LDG, we realize that substantial conceptual, statistical, and computational challenges are associated with this task [52]. The complexity of the suggested models often makes it difficult to understand the consequences of the underlying assumptions. Ways of overcoming such challenges are to build on known ecological models (e.g. Lotka-Volterra equations) and evolutionary theory (e.g. Adaptive Dynamics theory) that has been studied extensively. The models should also be built and analyzed in a sequential manner of increased complexity to shed light on the consequences of the key model assumptions and their interactions. While it is not our aim to detail these and other methodological challenges here, we nevertheless highlight two basic inferential approaches that seem particularly promising. First, qualitative matching of multiple patterns gives an indication of whether the modeled processes can produce the patterns that we observe [15, 25, 41, 53]. Pattern matching is conceptually straightforward and easily allows combining the LDG with multiple observed secondary patterns to compare alternative model or parameter choices. Second, models like the ones suggested above can be fitted to a range of patterns in data using simulation-based methods such as **Approximate Bayesian Computation** [54-57] or synthetic likelihood [58, 59]. Regardless of which inferential approach is used, any empirical patterns that a model is unable to reproduce can be instructive in the iterative process of model improvement.

Concluding remarks

Progress in understanding the processes that underlie LDG patterns and associated diversity patterns has been slow (see also Outstanding Questions). We repeat calls for a transition in biodiversity research, translating verbal models into a unified mechanistic framework that can be implemented in quantitative computer simulations [52, 53, 60]. In such a framework,

researchers can focus on measuring and inferring the ecological and evolutionary processes that govern the interaction of organisms with each other and their environment in time and space, which must ultimately underpin the LDG. By applying this framework, hidden assumptions in current hypotheses are exposed, revealing how the hypotheses relate to each other and how they might be distinguished (Table 1, Figure 1). More importantly, this framework is a roadmap for flexible eco-evolutionary simulation models (Box 1-2) that can generate a rich set of empirical patterns from the same underlying processes. We believe that this ability to produce multiple diagnostic patterns will be crucial for inference (Box 3), and ultimately for converting the available data into new knowledge about macroecology and macroevolution. Challenges associated with model construction and the way models are confronted with data will arise, but such challenges are inherent and inevitable to all sciences that deal with complex systems. We are confident that, with time, these challenges can be addressed, and models combining realistic spatiotemporal environmental templates with trait based eco-evolutionary implementation under an iterative procedure of model design, evaluation and improvement, will advance our understanding and quantitative inference of the processes underlying the LDG.

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Literature Cited

1. Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. American Naturalist 163 (2), 192-211.
2. Mannion, P.D. et al. (2014) The latitudinal biodiversity gradient through deep time. Trends in Ecology & Evolution 29 (1), 42-50.
3. Lomolino, M.V. et al. (2017) Biogeography: biological diversity across space and time, Fifth Edition edn.
4. Fine, P.V.A. (2015) Ecological and evolutionary drivers of geographic variation in species diversity. Annual Review of Ecology, Evolution, and Systematics 46, 369-392.
5. Currie, D.J. et al. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters 7 (12), 1121-1134.
6. Hawkins, B.A. et al. (2003) Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. Ecology 84 (6), 1608-1623.
7. Valentine, J.W. and Jablonski, D. (2015) A twofold role for global energy gradients in marine biodiversity trends. Journal of Biogeography 42 (6), 997-1005.
8. Fritz, S.A. et al. (2016) Twenty-million-year relationship between mammalian diversity and primary productivity. Proceedings of the National Academy of Sciences of the United States of America 113 (39), 10908-10913.
9. Rohde, K. (1992) Latitudinal gradients in species-diversity - the search for the primary cause. Oikos 65 (3), 514-527.
10. Ricklefs, R.E. (2006) Global variation in the diversification rate of passerine birds. Ecology 87 (10), 2468-2478.
11. Mittelbach, G.G. et al. (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecology Letters 10 (4), 315-331.
12. Wiens, J.J. et al. (2010) Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13 (10), 1310-1324.
13. Marin, J. et al. (2018) Evolutionary time drives global tetrapod diversity. Proceedings of the Royal Society B-Biological Sciences 285 (1872).
14. Servedio, M.R. et al. (2014) Not just a theory-the utility of mathematical models in evolutionary biology. Plos Biology 12 (12).
15. Grimm, V. et al. (2005) Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310 (5750), 987-991.
16. Hurlbert, A.H. and Stegen, J.C. (2014) On the processes generating latitudinal richness gradients: identifying diagnostic patterns and predictions. Frontiers in Genetics 5.
17. Vellend, M. (2016) The Community of Ecological Communities.
18. Kraft, N.J.B. et al. (2015) Community assembly, coexistence and the environmental filtering metaphor. Functional Ecology 29 (5), 592-599.
19. Leprieur, F. et al. (2016) Plate tectonics drive tropical reef biodiversity dynamics. Nature Communications 7.
20. Badgley, C. et al. (2017) Biodiversity and topographic complexity: modern and geohistorical perspectives. Trends in Ecology & Evolution 32 (3), 211-226.
21. Pellissier, L. et al. (2018) Are global hotspots of endemic richness shaped by plate tectonics? Biological Journal of the Linnean Society 123 (1), 247-261.
22. Urban, M.C. and Skelly, D.K. (2006) Evolving metacommunities: toward an evolutionary perspective on metacommunities. Ecology 87 (7), 1616-1626.
23. Urban, M.C. and De Meester, L. (2009) Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. Proceedings of the Royal Society B-Biological Sciences 276 (1676), 4129-4138.

24. Storch, D. et al. (2018) The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity-diversity relationship. Ecology Letters 21 (6), 920-937.
25. Hurlbert, A.H. and Stegen, J.C. (2014) When should species richness be energy limited, and how would we know? Ecology Letters 17 (4), 401-413.
26. Janzen, D.H. (1967) Why mountain passes are higher in tropics. American Naturalist 101 (919), 233-&.
27. Ghalambor, C.K. et al. (2006) Are mountain passes higher in the tropics? Janzen's hypothesis revisited. Integrative and Comparative Biology 46 (1), 5-17.
28. Sheldon, K.S. et al. (2018) Fifty years of mountain passes: a perspective on Dan Janzen's classic article. American Naturalist 191 (5), 553-565.
29. MacArthur, R.H. (1972) Geographical ecology.
30. Ben-Eliahu, M.N. and Safriel, U.N. (1982) A comparison between species diversities of polychaetes from tropical and temperate structurally similar rocky inter-tidal habitats. Journal of Biogeography 9 (5), 371-390.
31. Antonelli, L.A. et al. (2015) An engine for global plant diversity: highest evolutionary turnover and emigration in the American tropics. Frontiers in Genetics.
32. Rabosky, D.L. et al. (2018) An inverse latitudinal gradient in speciation rate for marine fishes. Nature 559 (7714), 392-395.
33. Allen, A.P. et al. (2006) Kinetic effects of temperature on rates of genetic divergence and speciation. Proceedings of the National Academy of Sciences of the United States of America 103 (24), 9130-9135.
34. Brown, J.H. et al. (2004) Toward a metabolic theory of ecology. Ecology 85 (7), 1771-1789.
35. Hubbell, S.P. (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press.
36. Wiens, J.J. and Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. Trends in Ecology & Evolution 19 (12), 639-644.
37. Wiens, J.J. and Graham, C.H. (2005) Niche conservatism: Integrating evolution, ecology, and conservation biology. Annual Review of Ecology Evolution and Systematics 36, 519-539.
38. Gillooly, J.F. and Allen, A.P. (2007) Linking global patterns in biodiversity to evolutionary dynamics using metabolic theory. Ecology 88 (8), 1890-1894.
39. Jocque, M. et al. (2010) Climatic control of dispersal-ecological specialization trade-offs: a metacommunity process at the heart of the latitudinal diversity gradient? Global Ecology and Biogeography 19 (2), 244-252.
40. Dynesius, M. and Jansson, R. (2000) Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. Proceedings of the National Academy of Sciences of the United States of America 97 (16), 9115-9120.
41. Rangel, T.F. et al. (2018) Modeling the ecology and evolution of biodiversity: Biogeographical cradles, museums, and graves. Science 361 (6399).
42. Davies, T.J. et al. (2011) Neutral biodiversity theory can explain the imbalance of phylogenetic trees but not the tempo of their diversification. Evolution 65 (7), 1841-1850.
43. Descombes, P. et al. (2018) Linking species diversification to palaeo-environmental changes: a process-based modelling approach. Global Ecology and Biogeography 27 (2), 233-244.
44. Muller, R.D. et al. (2008) Long-term sea-level fluctuations driven by ocean basin dynamics. Science 319 (5868), 1357-1362.
45. Chalmandrier, L. et al. (2018) Comparing spatial diversification and meta-population models in the Indo-Australian Archipelago. Royal Society Open Science 5 (3).
46. Brännström, A. et al. (2012) Modelling the ecology and evolution of communities: a review of past achievements, current efforts, and future promises. Evolutionary Ecology Research 14 (5), 601-625.
47. Cabral, J.S. and Kreft, H. (2012) Linking ecological niche, community ecology and biogeography: insights from a mechanistic niche model. Journal of Biogeography 39 (12), 2212-2224.

48. Pontarp, M. and Wiens, J.J. (2017) The origin of species richness patterns along environmental gradients: uniting explanations based on time, diversification rate and carrying capacity. Journal of Biogeography 44 (4), 722-735.
49. Urban, M.C. (2011) The evolution of species interactions across natural landscapes. Ecology Letters 14 (7), 723-732.
50. Roy, K. and Goldberg, E.E. (2007) Origination, extinction, and dispersal: Integrative models for understanding present-day diversity gradients. American Naturalist 170, 71-85.
51. Pontarp, M. and Petchey, O.L. (2016) Community trait overdispersion due to trophic interactions: concerns for assembly process inference. Proceedings of the Royal Society B-Biological Sciences 283 (1840).
52. Connolly, S.R. et al. (2017) Process, Mechanism, and modeling in macroecology. Trends in Ecology & Evolution 32 (11), 835-844.
53. Cabral, J.S. et al. (2017) Mechanistic simulation models in macroecology and biogeography: state-of-art and prospects. Ecography 40 (2).
54. Sisson, S.A. et al. (2007) Sequential Monte Carlo without likelihoods. Proceedings of the National Academy of Sciences of the United States of America 104 (6), 1760-1765.
55. Beaumont, M.A. (2010) Approximate Bayesian Computation in Evolution and Ecology. Annual Review of Ecology, Evolution, and Systematics, Vol 41 41, 379-406.
56. Hartig, F. et al. (2011) Statistical inference for stochastic simulation models - theory and application. Ecology Letters 14 (8), 816-827.
57. Blum, M.G.B. et al. (2013) A comparative review of dimension reduction methods in Approximate Bayesian Computation. Statistical Science 28 (2), 189-208.
58. Wood, S.N. (2010) Statistical inference for noisy nonlinear ecological dynamic systems. Nature 466 (7310), 1102-U113.
59. Hartig, F. et al. (2014) Technical note: Approximate Bayesian parameterization of a process-based tropical forest model. Biogeosciences 11 (4), 1261-1272.
60. Gotelli, N.J. et al. (2009) Patterns and causes of species richness: a general simulation model for macroecology. Ecology Letters 12 (9), 873-886.